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A suspension feeding anomalocarid from the early Cambrian

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Large, actively swimming suspension feeders evolved several times in Earth's history, arising independently from groups as diverse as sharks, rays, stem teleost fishes¹, and in mysticete whales². Animals occupying this niche have not, however, been identified from the early Palaeozoic. Anomalocarids, a group of stem arthropods that were the largest nektonic animals of the Cambrian and Ordovician, are generally thought to have been apex predators³⁻⁵. Here we describe new material of *Tamisiocaris borealis*⁶, an anomalocarid from the early Cambrian (Series 2) Sirius Passet Fauna of North Greenland, and propose that its frontal appendage is specialized for suspension feeding. The appendage bears long, slender and equally spaced ventral spines furnished with dense rows of long and fine auxiliary spines. This suggests that it was a microphagous suspension feeder, using its appendages for sweep-net capture of food items down to 0.5 mm, within the size range of mesozooplankton such as copepods. *Tamisiocaris* demonstrates that large, nektonic suspension feeders first evolved during the Cambrian Explosion, as part of the adaptive radiation of anomalocarids. The presence of suspension-feeders in the early Cambrian, together with evidence for a diverse pelagic community containing phytoplankton^{7,8} and mesozooplankton^{7,9,10}, indicates the existence of a complex pelagic ecosystem¹¹ supported by high primary productivity and nutrient flux^{12,13}. Cambrian pelagic ecosystems appear to have been more modern than previously believed.

Tamisiocaris borealis, from the early Cambrian Sirius Passet fauna of North Greenland, has previously been described as a possible anomalocarid on the basis of a disarticulated frontal appendage⁶. New fossils not only substantiate the anomalocarid affinities of *Tamisiocaris*, but also suggest that it was adapted to prey microphagously on mesozooplankton.

Tamisiocaris borealis is now known from five isolated frontal appendages and two appendages associated with a head shield. Frontal appendages (Fig. 1)

1 measure ≥ 120 mm in length, comparable in size to the later *Anomalocaris*
2 *canadensis*¹⁴, whereas the total size of the body is not known. As in other
3 anomalocarids, the appendage consists of discrete, sclerotized articles. All
4 specimens are preserved with the ventral spines parallel to the bedding plane,
5 and the articles show no evidence of distortion due to compaction. It is therefore
6 assumed that the articles were transversely compressed, with an oval cross
7 section in life. The appendage consists of at least 18 articles, versus 14 in, for
8 example, *A. canadensis*. Articles are separated by triangular arthrodial
9 membranes (Extended Data Fig. 2b,c). These extend almost to the dorsal margin
10 of the appendage; ventrally, the membrane is 33-50% the length of the articles,
11 suggesting a well-developed flexural ability.

12 The appendage curves downward distally, with the strongest curvature
13 around the second and third article. The first article is straight, and longer than
14 the next three combined. It bears a single pair of ventral spines near its distal
15 margin, which are stout and angled backwards (Fig. 1a) as in *Anomalocaris*
16 *briggsi*⁵. The next 17 articles each bear pairs of long and delicate ventral spines
17 inserted at the mid-length of the article. These are evenly spaced along the
18 appendage about 5-6 mm apart. The spines diverge ventrally such that each pair
19 forms an inverted V-shape. Unlike *A. canadensis*, in which longer and shorter
20 spines alternate and taper distally, the ventral spines are all of similar length,
21 measuring 26-27.5 mm along the full length of the appendage (Fig. 1a,b,
22 Extended Data Fig. 1-3). A similar condition is seen in *A. briggsi*. The ventral
23 spines curve posteriorly, again as in *A. briggsi*, but unlike any other
24 anomalocarids. Individual spines appear flattened, with a median rod and
25 thinner lamellar margins (Extended Data Fig. 1c). In addition, ventral spines are

1 frequently kinked, and sometimes broken, suggesting that they were weakly
2 sclerotized and flexible.

3 As in many other anomalocarids^{5,15}, the anterior and posterior margins of
4 the ventral spines bear auxiliary spines (Fig. 1c, Extended Data Fig. 1c, 2d, 3), but
5 they are unusually long in *Tamisiocaris* —measuring 4.2-5.0 mm in length— and
6 extremely slender. Auxiliary spines form a comblike array, being spaced 0.3-.85
7 mm apart, with a median spacing of 0.49 mm. The length and spacing are such
8 that adjacent spine combs between spines would overlap or interdigitate.

9 One specimen consists of two associated appendages in subparallel
10 orientation (Extended Data Fig. 4). Proximally, they join a large, elliptical head
11 shield. The head shield is larger than in *Anomalocaris canadensis*, but is not
12 enlarged to the same degree as seen in *Peytoia nathorsti* and *Hurdia victoria*.
13 Eyes are not preserved.

14 The affinities of *Tamisiocaris* were examined in a cladistic analysis to
15 explore its position within the anomalocarids. The analysis recovers a clade
16 consisting of *Tamisiocaris borealis* and *Anomalocaris briggsi* (Fig. 3). This clade,
17 which we name the Cetiocaridae (cetus: whale, shark or other large marine
18 animal; and caris: sea crab), is diagnosed by long, slender, and recurved ventral
19 spines, and the presence of numerous auxiliary spines. *Tamisiocaris* is more
20 specialized, however, in having flexible ventral spines and densely packed
21 auxiliary spines. The cetiocarids are a sister to Hurdiidae, a clade containing
22 *Hurdia victoria*, *Peytoia nathorsti*, and related species. Outside these taxa lies a
23 clade of plesiomorphic forms including *Anomalocaris canadensis*, *A. saron*,
24 *Amplectobelua* spp., and relatives.

25 The hypothesis that *Tamisiocaris borealis* engaged in suspension feeding

1 can be evaluated by comparisons with extant analogues (Extended Data Figure
2 5). Suspension feeding crustaceans, such as cirripedes (barnacles), atyid shrimp,
3 copepods, cladocerans, mysids and euphausiaceans (krill) share a suite of
4 adaptations for sieving particles out of the water column that are also found in
5 the Cetiocaridae (Extended Data Figure 5). These include appendages with (i)
6 very elongate, flexible setae and/or setules and (ii) regular spacing, and (iii)
7 close spacing of setae/setules. These features create a net with a regular mesh
8 size that efficiently traps all particles above a threshold set by the setal spacing.
9 The feeding limbs sieve particles out of the water, concentrate them by
10 contraction, and carry them to the mouth¹⁶. The suspension feeding apparatuses
11 of vertebrates have a similar morphology. Suspension-feeding teleosts and some
12 sharks use a mesh formed by long, slender, and closely spaced gill rakers. The
13 feeding apparatus of mysticete whales consists of arrays of baleen plates that
14 wear into elongate fringes¹⁷.

15 The mesh size of the capture apparatus is closely related to prey size:
16 Right whales specialise on small copepods (fringe diameter 0.2 mm) while blue
17 whales (fringe diameter 1 mm) feed on larger krill¹⁸. A survey of diverse
18 suspension feeders, from cladocerans to blue whales, shows a linear relationship
19 between mesh size and minimum prey size (Fig. 4). While larger prey can be
20 captured, the bulk of the prey is close to the mesh size of the suspension
21 apparatus.

22 Based on the morphologies seen in modern animals, a suspension-feeding
23 anomalocarid would be predicted to have evolved a setal mesh, with large
24 appendages bearing long, flexible setae to increase capture area, with close,
25 regular setal spacing. This is indeed the morphology observed in *Tamisiocaris*.

1 Furthermore, one can use the mesh dimensions to predict the size of the prey
2 caught by *Tamisiocaris*. Spacing of the auxiliary spines in *T. borealis* suggests that
3 it could suspension feed items from the water column down to 0.5 mm, while
4 linear regression from extant suspension feeders (Fig. 4) predicts a slightly
5 larger minimum particle size of 0.71 mm. Known mesozooplankton, from small
6 carbonaceous fossil assemblages from the Cambrian Series 2^{9,10}, include isolated
7 feeding appendages from crustaceans, including putative copepods. Based on
8 comparisons with mandibles of modern counterparts¹⁰ the largest known
9 specimens reached diameters of 1.5 to 2.7 mm. We hypothesise that feeding was
10 accomplished by alternate sweeping of the appendages, with entrapped prey
11 being sucked¹⁹ up by the oral cone (Supplementary information animation 1 and
12 2).

13 In the context of the phylogenetic analysis presented here (Fig. 3),
14 different anomalocarid clades evolved distinct frontal appendage morphologies
15 and feeding strategies. Primitive forms such as *Anomalocaris canadensis* had
16 raptorial appendages with stout, trident-like spines, well-suited to impaling
17 large, free-swimming or epifaunal prey³ (Extended Data Fig. 6a,b). *Amplectobelua*
18 had pincer-like appendages²⁰ (Extended Data Fig. 6c,d) that would have been
19 effective in seizing and tearing apart relatively large, slow-moving animals. In
20 hurdiids, the appendages bear opposing pairs of spines, which may have
21 functioned as jaws or in sediment sifting¹⁵ (Extended Data Fig. 6e,f). Finally,
22 cetiocarid frontal appendages are specialized as sweep nets (Extended Data Fig.
23 6g,h). This extraordinary range of appendage morphologies shows that, far from
24 being a failed experiment, anomalocarids staged a major adaptive radiation
25 during the Cambrian Explosion, evolving to fill a range of niches as nektonic

1 predators, much like the later radiations of vertebrates²¹ and cephalopods²² by
2 also becoming secondary suspension feeders.

3 The existence of suspension feeding in anomalocarids also has
4 implications for the structure of early Cambrian pelagic food webs (Extended
5 Data Fig. 7). It had been assumed that a diverse planktonic fauna and suspension
6 feeding animals did not evolve until the late Cambrian²³ and thus the complexity
7 of the pelagic food web evolved in a delayed, piecemeal fashion. However, the
8 discovery of large suspension feeders in the early Cambrian suggests a well-
9 developed pelagic biota supported by high primary productivity and abundant
10 mesozooplankton, because large animals can only exploit small prey when they
11 exist at high densities. Whales, whale sharks and basking sharks exploit highly
12 productive areas such as upwelling zones and seasonal plankton blooms at high
13 latitudes²⁴. This general observation holds for all microphagous suspension
14 feeders ranging from cladocerans, to anchovies, to red salmon, to blue whales: a
15 high density of food particles is required to sustain an actively swimming
16 suspension feeder.

17 Other evidence for high primary productivity in the Cambrian includes
18 vast deposits of phosphorites and increased terrestrial nutrient flux^{12,13,25}, imply
19 that high productivity may have been a global phenomenon in the Cambrian.
20 Furthermore, the Cambrian also witnessed a radiation of spiny acritarchs, which
21 are thought to have lived as microscopic phytoplankton, replacing larger
22 Neoproterozoic benthic forms^{7,8}. Complex minute crustacean feeding
23 appendages also occur in lower and middle-upper Cambrian rocks^{9,10},
24 demonstrating the presence of diverse mesozooplankton, preying on
25 phytoplankton. Abundant vetulicolians in Sirius Passet²⁶ (with hundreds of

1 specimens collected on recent expeditions) may also have been suspension
2 feeding upon phytoplankton (Extended Data Fig. 6). One tier up, *Tamisiocaris*
3 would have preyed upon the mesozooplankton as would the common nektonic
4 arthropod *Isoxys volucris*²⁷. Other pelagic predators known from *Lagerstätten*
5 elsewhere would also have fed on mesozooplankton, including ctenophores,
6 cnidarians, chaetognaths¹¹ and pelagic arthropods²⁸ (Extended Data Fig. 7). The
7 Cambrian pelagic food web was therefore highly complex^{28,29}, containing
8 multiple trophic levels, including pelagic predators¹¹ and multiple tiers of
9 suspension-feeders. This underscores the remarkable speed with which a
10 modern food chain was assembled during the Cambrian Explosion.

11 Finally, the discovery of a suspension feeding anomalocarid has
12 implications for debates concerning the predictability of evolution, or lack
13 thereof. One view holds that evolution is ultimately unpredictable³⁰. The striking
14 convergence between *Tamisiocaris* and extant suspension feeders, however,
15 suggests that while different groups occupy ecological niches at different times,
16 the number of viable niches and viable strategies for exploiting them are limited.
17 Furthermore, the derivation of the suspension-feeding *Tamisiocaris* from a large
18 apex predator parallels the evolution of suspension feeding pachycormid fish^{1,21},
19 sharks and whales². In each case, suspension feeders evolved from nektonic
20 macropredators. This suggests that evolution is canalized not only in terms of
21 outcomes, but in terms of trajectories. The result is that independent
22 evolutionary experiments by animals as different as anomalocarids, fish and
23 whales have converged on broadly similar outcomes.

24

25 METHODS SUMMARY

1 Specimens were collected in the field and photographed in the lab, coated or
 2 uncoated and submerged in water. A digital reconstruction of the *Tamisiocaris*
 3 feeding appendage were made in order to infer the range of motions. The
 4 suspension mesh diameter and prey width were collected from literature on
 5 extant suspension feeders to depict the linear relationship between these (see
 6 supplementary Methods). A cladistic analysis containing 31 taxa and 51
 7 characters was collated and analysed in PAUP* 4.0 b10 and TNT (see
 8 Supplementary Information).

9

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6

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17
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21

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23 www.nature.com/reprints. The authors declare no competing financial interests.
24 Readers are welcome to comment on the online version of the paper.
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27

28 **Figure 1 | *Tamisiocaris borealis* Daley and Peel, 2010 frontal appendages**
29 **from Sirius Passet, Lower Cambrian, North Greenland.** **a**, Isolated and
30 relatively complete appendage, MGUH 30500 (Geological Museum at the
31 University of Copenhagen). **b**. Isolated appendage, preserving auxiliary spines in
32 great detail, MGUH 30501. **c**, detail of spine in **b**. All specimens photographed
33 submerged in water with high angle illumination.
34

35 **Figure 2 | A digital reconstruction of *Tamisiocaris*.** **a**. Single appendage
36 indicating the articulating membranes (Am), articles (Art), spines (Sp) and
37 auxiliary spines (As). **b**. Possible sequence of movement of the frontal

appendage of *Tamisiocaris*. See also Extended Data movies 1 and 2.

Figure 3 | Phylogeny of anomalocarids. Strict consensus of 91 trees derived from an analysis of 31 taxa and 54 characters using parsimony in PAUP* 4.0b10. *Tamisiocaris borealis* forms a clade with *Anomalocaris briggsi*, here named Cetiocaridae.

Figure 4 | Diagram depicting the relationship between suspension mesh size and the food items consumed by suspension feeders. *Tamisiocaris* is indicated by the dotted line based on a mesh width of 0.51 mm. The diagram is collated from a range of modern suspension feeders, see Online Methods section.

Methods section

Material. Five specimens of *Tamisiocaris borealis* (MGUH 30500-30504) were collected in situ from the main exposure (Locality 1) (fig. 1, Extended Data Figure 1-3) of Sirius Passet^{1,2,3}, Nansen Land, North Greenland during expeditions in 2009 and 2011. The type specimen, described by Daley and Peel (MGUH 29154)³, was collected on an earlier expedition.

Photography. Specimens were photographed, using a Nikon d800, with a Nikon micro Nikkor 105 mm F/2.8G AF-S VR and Nikon AF micro Nikkor 60 mm F/2.8D lens in low angle light using an LED light source after coating with MgO smoke. Specimens were also photographed submerged in water with high angle polarized lighting in order to maximize reflectivity of the specimen. Images were cropped and image contrast and colour levels were adjusted in Adobe Photoshop CS6.

Digital reconstruction. Proportions of articles, spine length, and the extent of arthrodial membrane in the reconstruction are based on a single schematic line

1 drawing created from interpretative drawings of the specimens. This was used as a
2 blueprint to model a subdivision surface mesh in Cheetah3D 6.2.1. The reconstruction
3 was rigged with an armature of 19 bones, using forward kinematics. The bones were
4 laid along the main axis of the articles in the dorsal quarter of the articles, where the
5 pivot joints must have been placed judging from the extent of the arthrodial
6 membrane (Extended Data Fig. 2). The mesh was bound to the armature with full
7 vertex weight assigned to the articles, less than half vertex weight to the adjacent
8 arthrodial membrane area. This ensured rigid behavior of the articles upon rotation.
9 For the animation sequence, bones were rotated to the maximum extension (Fig. 2,
10 supplemental data movie 1 and 2) permitted by the arthrodial membrane areas
11 (Extended Data Fig. 2).

12

13 **Comparisons with modern suspension feeders.** Published records of the mesh size
14 and width of the diet in various suspension feeders were collated and plotted in a
15 double logarithmic diagram in order to investigate their possible correlation. Included
16 taxa included, cladocerans: *Chydorus spaericus*⁴, *Daphnia hyalina*⁴, *D. magna*⁴, *D.*
17 *galeata*⁴; Mysids: *Mesodopsis woolridgei*⁵, *Rhopalophthalmus terranatalis*⁵; Krill:
18 *Euphausia superba* (references); Japanese anchovy, *Engraulis japonicus*⁶; Pacific
19 Round Herring, *Etrumeus teres*⁶, Rainbow trout, *Oncorhynchus mykiss*⁷; Greater
20 flamingo, *Phoenicopterus antiquorum*⁸; Lesser flamingo, *Phoenicomaia minor*⁸;
21 Whale Shark, *Rhincodon typus*⁹; Mysticete whales: Right Whale¹⁰, Blue Whale¹⁰,
22 Bowhead whale¹¹. For baleen whales, the effective mesh size of the baleen plates is
23 contingent on the speed of water movement across the baleen plate. In bow head
24 whales, speeds of 5 km/h while feeding is reported, thus the fastest measured speed of
25 100 cm/s measured across multiple baleen plates was used as effective mesh diameter

1 (inter fringe diameter) while for right whale and blue whale the diameter of the baleen
 2 fringe was used as a proxy for filter mesh size.
 3 We did a linear ($y = 1.6675x$; $R^2 = 0.26843$) and power (Lower bound: $y =$
 4 $1.4452x^{1.0083}$; $R^2 = 0.91627$, Upper bound: $y = 11.772x^{0.8928}$
 5 $R^2 = 0.8708$) regression, which are similar in trajectory.

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36 37 38 39 **Extended Data figure 1 | *Tamisiocaris borealis* MGUH 30500, frontal**

40 **appendage. a.** Part photographed in low angle lighting coated with MgO. **b.**
 41 Camera lucida drawing with indications of spines (s1-s15); spines, broken at the
 42 base (Bs). **c.** Detail of spine preserving auxiliary spines in relief (arrowed).

43

44

1 **Extended Data figure 2 | *Tamisiocaris borealis* MGUH 30500, frontal**
2 **appendage. a.** Part, photographed submerged in water and with high angle
3 illumination. **b.** Counterpart, displaying articulating membranes across the
4 appendage indicated by their relatively lower reflectivity. **c.** Detail of **b**, and the
5 articulating membranes (Am) and articles (Art) along the mid section of the
6 appendage. **d.** Detail of broken spine in **b**, displaying auxiliary spines.

7
8 **Extended Data figure 3 | *Tamisiocaris borealis* MGUH 30501 frontal**
9 **appendage with well preserved auxiliary spines. a.** Part. **b.** Detail of auxiliary
10 spines in **a**. **c.** Schematic drawing of MGUH 30501, from a combination of part
11 and counterpart. **d.** Counterpart. **e.** Detail of **d** showing regular arrangement of
12 auxiliary spines.

13
14 **Extended Data figure 4 | MGUH 30502 frontal appendages and head shield**
15 **assemblage, lateral view. a.** Part. **b.** Camera lucida drawing of the part
16 indicating the head shield (Hs), left frontal appendage (Lfa) and right frontal
17 appendage (Rfa). Partially superimposed on the specimen is the other arthropod
18 *Buenaspis* (Ba). **c.** Detail of distal section of frontal appendages in counterpart. **d.**
19 detail of head shield.

20
21 **Extended Data figure 5 | Modern crustacean suspension feeders. a.** The
22 Northern krill, *Meganyctiphanes norvegica* (Image credit: Wikipedia/Øystein
23 Paulsen). Insert: reconstruction of the thoracic region of the krill, *Euphausia*
24 *suberba*, from Barkley (1940). **b.** Proximal elements of the thoracopods in *E.*
25 *suberba* (Image credit, Uwe Kils). **c.** Distal elements of the thoracopods in *E.*

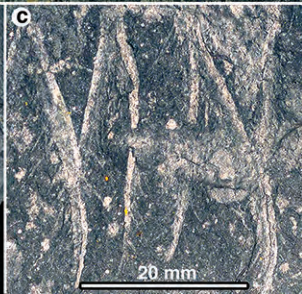
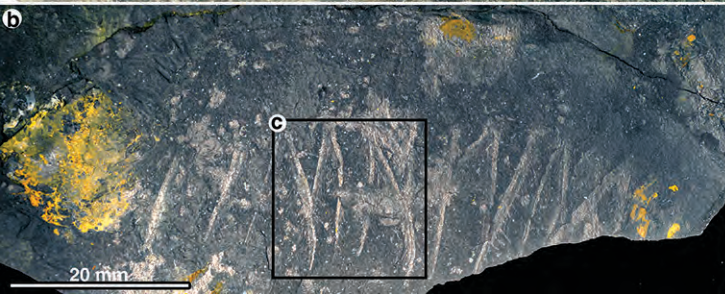
1 *suberba* (Image credit, Uwe Kils). **d.** The filter basket in an undetermined mysid
2 (Image credit Wikipedia/Uwe Kils). **e.** Thoracopod from the cirripede
3 *Darwiniella angularis* Chen, Lin and Chan 2012, with permission from the
4 authors.

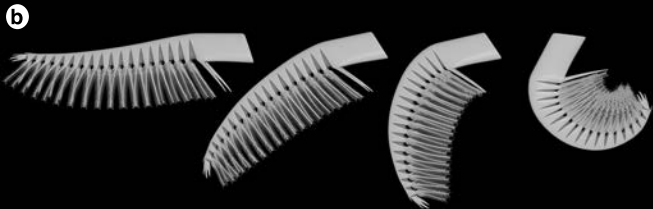
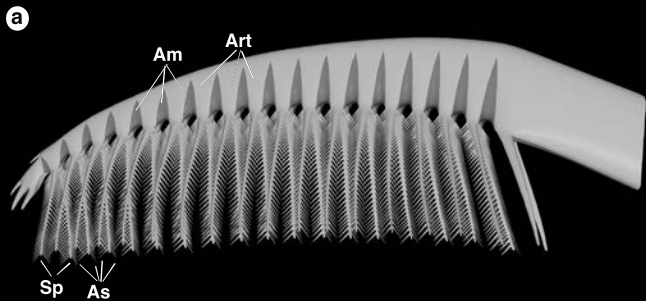
5
6 **Extended Data figure 6 | Schematic drawings of different anomalocarid**

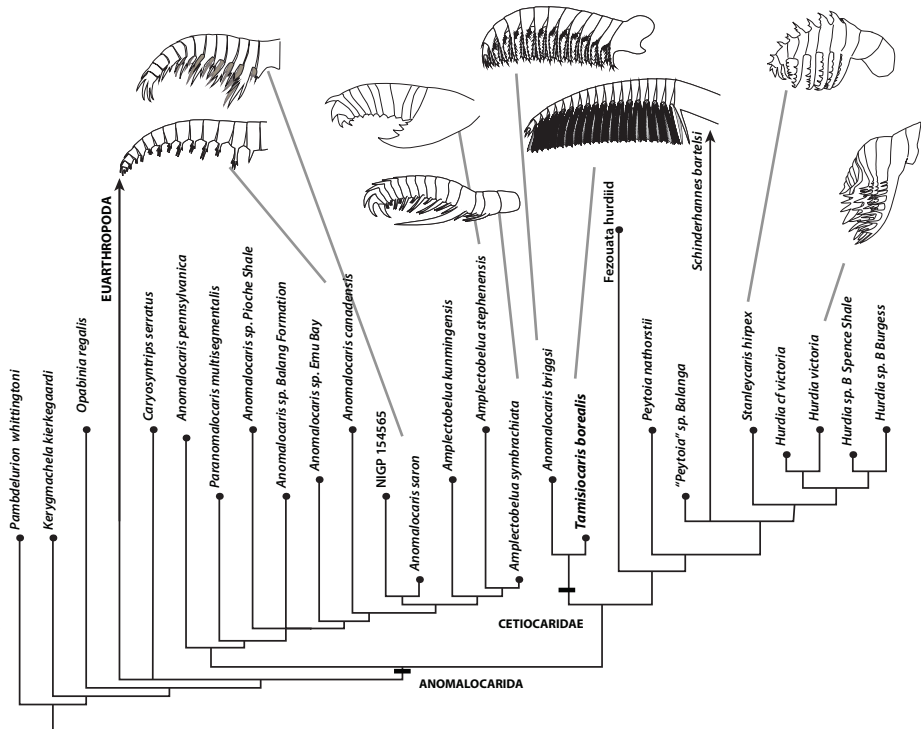
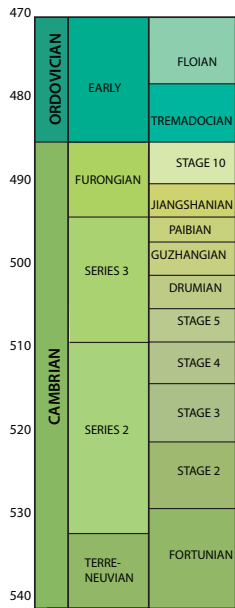
7 **frontal appendages. a.** *Tamisiocaris borealis*, **b.** *Anomalocaris briggsi*, **c.**
8 *Anomalocaris canadensis*, **d.** *A. cf. saron*, NIGP 154565, **e.** *Amplectobelua*
9 *symbrachiata*, **f.** *Amplectobelua stephenensis*, **g.** *Hurdia victoria*, **h.** *Stanleycaris*
10 *hirpex*.

11
12 **Extended Data figure 7 | A schematic overview of some of the known**

13 **components the early Cambrian pelagic food web.** At the base of the food
14 chain was phytoplankton in the form of acritarchs and most likely other forms
15 with no apparent fossil record. Diverse mesozooplankton were present as
16 copepod and branchiopod-like crustaceans feeding on phytoplankton, along with
17 vetulicolians, which exhibit a morphology suggesting suspension feeding similar
18 to basal chordates. Larger pelagic predators such as chaetognaths, larger
19 arthropods and potentially also ctenophores preyed upon the mesozooplankton.
20 *Tamisiocaris* would similarly have fed on the mesozooplankton. The presence of
21 a large nektonic suspension feeder suggests a high abundance of primary
22 producers and mesozooplankton. Other anomalocarids, such as *Anomalocaris*
23 and *Amplectobelua* were present as some of the macrophagous apex predators at
24 this time.







Planktonic prey width

Krill,
Small fish



Copepods,
Mysids,
Cladocerans



Eucaryotic
algae



Bacteria



Meso

Micro

Nano

Pico

